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An Agent-Based Model to Investigate the Roles of Attractive and Repellent Pheromones in Ant Decision Making During Foraging

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Abstract

Pharaoh's ants organise their foraging system using three types of trail pheromone. All previous foraging models based on specific ant foraging systems have assumed that only a single attractive pheromone is used. Here we present an agent-based model based on trail choice at a trail bifurcation within the foraging trail network of a Pharaoh's ant colony which includes both attractive (positive) and repellent (negative) trail pheromones. Experiments have previously shown that Pharaoh's ants use both types of pheromone. We investigate how the repellent pheromone affects trail choice and foraging success in our simulated foraging system. We find that both the repellent and attractive pheromones have a role in trail choice, and that the repellent pheromone prevents random fluctuations which could otherwise lead to a positive feedback loop causing the colony to concentrate its foraging on the unrewarding trail. An emergent feature of the model is a high level of variability in the level of repellent pheromone on the unrewarding branch. This is caused by the repellent pheromone exerting negative feedback on its own

deposition. We also investigate the dynamic situation where the location of the food is changed after foraging trails are established. We find that the repellent pheromone has a key role in enabling the colony to refocus the foraging effort to the new location. Our results show that having a repellent pheromone is adaptive, as it increases the robustness and flexibility of the colony's overall foraging response.

Keywords: self-organisation, robustness, agent model, foraging trail, Pharaoh's ant

Introduction

Collective foraging by ants is one of the most impressive examples of co-operation in the natural world. In contrast to solitary animals where a forager usually collects food only for itself and its dependant offspring, an ant colony's foragers all increase their inclusive fitness by supplying food to the same "collective stomach." This has led to the evolution of many collective foraging strategies, from tandem running where one ant directly guides another (Wilson, 1959), to the massive pheromone-mediated raids of army ants (Chadab and Rettenmeyer, 1974) and the defoliation of entire trees by leaf-cutter ants (Cherrett, 1986). Key to collective foraging is the sharing of information, so that nestmates can be recruited by successful foragers to profitable food sources. The most dramatic example of this is mass recruitment via pheromone trails.

Recruitment along a pheromone trail and choice at a trail bifurcation have been modelled using differential equations (Beckers et al., 1992a; Goss et al., 1989; Nicolis and Deneubourg, 1999; Pasteels et al., 1987; Sumpter and Beekman, 2003) and using agent-based models (Crist and Haefner, 1994; Edelstein-Keshet et al., 1995; Haefner and Crist, 1994; Stickland et al., 1992; Stickland et al., 1993). However, these models have assumed that mass recruitment involves just one type of trail pheromone, a positive attractive one. In contrast, Pharaoh's ants, *Monomorium pharaonis,* use at least three types of foraging pheromone. Like many other ants, they forage in a branching network of pheromone trails (Sudd, 1960; Wilson, 1962). In the Pharaoh's ant this trail system is marked by

long-term attractive pheromones which are stable from day to day (Jackson et al., 2006). Within this trail system the ants lay a shorter-term attractive pheromone for rapid recruitment to food, but also a repellent pheromone with which they indicate unproductive trails (Robinson et al., 2005; Robinson et al., in press).

The effect of using a hypothesised repellent pheromone in addition to the attractive (positive) pheromone has been modelled in a theoretical foraging system (Britton et al., 1998; Stickland et al., 1999). This model predicted that using a repellent pheromone could make foraging more successful, because unsuccessful foragers could mark unrewarding areas with the repellent pheromone and prevent nestmates from wasting time re-exploring them. Here we investigate the role of the repellent pheromone empirically demonstrated in the Pharaoh's ant. Investigating foraging in the absence of one or other of these pheromones would be very difficult to contrive empirically. This modelling approach allows the testing of these hypothetical situations and gives us insights into the roles of the two pheromones.

Pheromone trail foraging is a self-organised "bottom up" process where the trails emerge as a result of local interactions between individual ants and their environment. Agent-based models are specified at the level of these local interactions, so we chose to apply this type of model to our system. Trail bifurcations are a key feature of ant trails, as a trail network can be seen as a set of connected bifurcations. Understanding ant behaviour at a single bifurcation, therefore, is essential to understanding how foraging is organised across the whole trail system. Our model deals with a single trail bifurcation, and is

parameterised using data from experiments on the Pharaoh's ant, in which the first repellent foraging trail pheromone was discovered (Robinson et al., 2005).

Model

The aim of this model is to investigate how the foraging success of a colony of trail-laying ants is affected by the combined use of attractive and repellent trail pheromones, and in particular to determine the advantages of having a repellent pheromone. In the model, ants choose between two outward trail branches at a trail bifurcation. One branch leads to food and the other does not. Success is quantified in terms of the proportion of ants which return to the nest fed, and the length of time taken to complete a foraging trip. The model investigates foraging in an established trail network and does not consider the initial formation of trails, which has been modelled elsewhere (Deneubourg et al., 1990; Jackson, 2005; Watmough and Edelstein-Keshet, 1995).

In this model each ant is specified as an 'agent'. These agents can be in one of a three behavioural states, *nest ant*, *unfed foraging ant*, *fed foraging ant,* (the boxes in fig. 1) and can make transitions between these states (the solid arrows in fig. 1) depending on inputs from the physical environment and information from its individual memory. Each agent (ant) has a memory which allows it to retain a record of four variables during its foraging

trip: a unique identifier for each agent, hunger status (fed or unfed), the position of agent within the environment and the direction in which the agent is heading.

The modelled environment consists of four cells: the nest, the stem of the trail, and two trail branches (fig. 2). One of the branches leads to a single inexhaustible source of food, while the other is unrewarding. In nature, Pharaoh's ants forage in networks containing many such bifurcations. The single bifurcation environment in this model is based on the environment in which many recent empirical experiments on foraging pheromones in Pharaoh's ants have been carried out (Jeanson et al., 2003; Robinson et al., 2005; Robinson et al., in press). In these experiments the stem and branches were formed from an elevated apparatus which the ants could not leave, although these cells could also be considered to be analogous to stretches of long-term trail, upon which the ants are foraging. In the latter case, it would be possible for some ants to leave the stem and branches to explore the surrounding space, however in this model we assume all ants stay on the trail.

In our model the agents are able to sense properties in the environment such as the presence of food or the level of pheromone, and also to change these properties, for example by laying more pheromone. In our model agents do not interact directly with other agents, only indirectly by affecting the environment. All ants are assumed to be capable of laying and detecting both pheromones.

Time is discretised, and a time-step is defined as the time taken for an ant to traverse one cell. This means it takes two time-steps for the ants to travel from the nest to the food if they make the correct choice at the bifurcation, and two more to travel back to the nest if they also make the correct choice on the way home. No time is allowed for food handling, or for searching the end of the unrewarding branch for food. The delay in return caused by these activities would be expected to have most effect during trail founding, rather than during the ongoing foraging which is considered in this model. In the course of a time-step, each agent in turn responds to its environment and behaves accordingly, undergoing one of the 6 processes outlined in fig.1. Ants which wait in the nest remain unchanged. As all ants are initially identical, they leave the nest in ID number order, at the rate determined by the traffic flow φ.

All unfed ants outside the nest follow the "Search for food" behavioural rules. First an ant uses its position and direction of heading to detect the environment ahead. The four possible options are that there is nest ahead, food ahead, dead-end ahead or a choice of routes ahead. If the nest is ahead the agent enters the nest and remains a nest ant. If there is food ahead, the agent becomes fed, turns round, and lays μ_{pos} units of positive pheromone. If there is a dead-end (no food and no more trail), the agent turns around and lays μ_{neg} units of negative pheromone.

If there is a choice of routes ahead, the agent must choose between the two available branches, and then move into the chosen cell. The agent may make a choice depending on

the pheromone concentrations, or may choose at random. The probability of the agent choosing at random is dependent on the error rate (ε), which is dependent on the angle to the options (θ). In nature, ant trail bifurcations are radially asymmetrical with the narrower angle pointing towards the nest (Acosta et al., 1993; Jackson et al., 2004). The effect of geometry is frequently ignored in models of trail choice (Goss et al., 1989; Millonas, 1992; Nicolis and Deneubourg, 1999). We included this angle-dependant error rate because even during very active foraging, there are always a small proportion of ants which will take the other branch, and due to inertia this should be affected by the angle through which the ants must turn. Returning ants are more likely to err by taking the stem which requires a small change in heading, than by taking the other branch which requires a large change in heading (fig 2). We parameterised these error rates from experimental data (See Suppl. Info).

In the model, if the agent does not choose a branch at random, then the two branches ahead are compared for attractiveness, down to a detection threshold, μ_{detect}. The effects of the two pheromones will be assumed to combine additively, so one unit of repellent pheromone would cancel out one unit of attractive pheromone, giving a branch attractiveness of zero (more details in Suppl. Info). If there is a difference, the ant chooses the most attractive branch; if there is no difference, the ant chooses at random. In previous trail choice models a range of choice functions have been used, including step functions where the more attractive branch is always chosen, above a threshold (Deneubourg et al., 1986; Haefner and Crist, 1994; Jackson, 2005), linear functions

relating attractiveness to choice (Stickland et al., 1992) and non-linear functions (Beckers et al., 1992a; Goss et al., 1989; Nicolis and Deneubourg, 1999), which include a saturation effect at high levels of attractiveness, although this saturation has been found to have little effect on choice models (Calenbuhr and Deneubourg, 1990). Watmough and Edelstein-Keshet (1995) compared step and non-linear functions in their model and found no significant differences in their results. Preliminary tests on our model found no qualitative and only minor quantitative differences between outputs using step, linear and non-linear choice functions. The trail choice function we used in the experiments described is a step function, i.e. after an angle-dependant chance of random choice the agents will always choose the more attractive branch if the difference between branches is above the detection threshold, μ_{detect}. Experimental results show that the both pheromones are volatile and can be detected before an ant reaches the substrate on which it was laid (Robinson et al., 2005; Robinson et al., in press), so it is biologically realistic for the agent to respond to the cells ahead of them. The pheromone is updated for the position at which the unfed agent started the time-step. If agents detect positive pheromone, they always lay more positive pheromone. In this way trails build up through positive feedback. There is extensive evidence for bidirectional trail laying once recruitment to a food source is in action, including in Pharaoh's ants (Beckers et al., 1992b; Hölldobler and Wilson, 1970; Jackson and Châline, 2007; Van Vorhis Key and Baker, 1986; Wilson, 1962).

All fed agents outside the nest are considered to be searching for the nest. The rules are the same as for searching for food, except that fed agents lay positive pheromone all the

time and if they detect food ahead, they simply turn around. The assumption that a small number of fed ants will take a wrong turn on their route home is supported by parameterisation experiments (Suppl. Info). The assumption that these ants continue to lay positive pheromone during these errors remains to be specifically tested, although it seems reasonable that these ants would at least initially be unaware of their error, and continue to behave as if they were on their way home.

The pheromones which have been laid during this time-step are all updated synchronously, and at the end of the time-step, the attractiveness (positive pheromone) or unattractiveness (negative pheromone) of each cell decays towards zero. We model this decay as an exponential function, asymptotic to zero (no effect) with decay parameter λ (Edelstein-Keshet et al., 1995; Jeanson et al., 2003). The positive and negative pheromones have the same rates of decay (Robinson et al., in press), so: $\lambda_{neg} = \lambda_{pos} = \lambda$.

Modelling Experiments: Methods

In these simulation experiments, the model was applied to the Pharaoh's ant foraging system, so the parameters were allocated values measured or estimated from real Pharaoh's ant foraging, as detailed below. Some parameters were then investigated within the context of the model. The model was implemented in Matlab Version 6.1.0.450 Release 12.1, © 1984-2001 The MathWorks, Inc.

Initial conditions

All the agents are initialised with the same set of variables, unfed and in the nest. In our simulation experiments, each agent makes only one trip. In real ant colonies many foragers make a second trip after transferring the food they have collected to nestmates or brood. Allowing for this in our model would only have made a difference if 'experienced' second trip agents behaved differently from 'naïve' first trip agents. Pharaoh's ant workers have very poor vision (Berndt and Eichler, 1987) and there is no evidence to suggest that they use internal memory to re-find routes. Rather, Pharaoh's ant colonies have an external memory in the form of their pheromone trails. This is what is simulated in our model, so we treat foraging trips independently.

As the simulation experiments are investigating foraging on an established trail, the environment is initialised with the route to food (stem and branch A) already attractive {20}, and the route to the unproductive dead end (branch B) unattractive {-20}. The nest is neutral. Preliminary simulation experiments showed that the final results are not qualitatively effected by the levels of initial attractiveness used. In the parts of experiment 2 and 4 where μ_{pos} and/or μ_{neg} are set to zero, the initial attractiveness and/or unattractiveness of the environment are also set to zero. Values and source for other constants and parameters are given in table 1.

Simulation Experiments

Within each experiment, each trial ran for 200 time-steps which corresponds to 20 minutes, except in experiment 3 which is discussed below. In experiment 1, 20 replicate simulation trials were carried out; for all other experiments 10 replicates of each trial were carried out.

Normal foraging: Experiment 1

In this experiment the parameters were set to the initial conditions given above. This allowed us to generate means and estimate variation between trials over the 20 replicates, to get an overall picture of the foraging pattern.

Pheromone strengths: Experiment 2

Here we first investigated the effect of the relative strengths of the 2 pheromones including trials where one or both pheromones had no effect, *i.e.* were effectively absent (see Table 2). Experiment 1 provided the control with both pheromones present; for comparability only the first 10 replicates were used.

Traffic flow rate: Experiment 3

The effects of the traffic flow rate were investigated. Both very low and very high numbers of ants per time-step were used: $\boldsymbol{\varphi}$ (ants per $\boldsymbol{\tau}$) = 8, 4, 2, 1, $^1/_2$, $^1/_4$, $^1/_8$, $^1/_{16}$, $^1/_{32}$. The total number of time-steps is set such that the total number of ants leaving the nest is 400.

Foraging in a dynamic environment: Experiment 4

Pharaoh's ants are scavengers and thrive in unpredictable environments. It has been hypothesised that one of the roles of the negative pheromone is to prevent foragers continuing to visit exhausted food sources (Robinson et al., 2005). In simulation experiment 4, we tested this hypothesis by changing the location of the food source to the opposite branch halfway through each trial in simulations: 4a had both attractive and repellent pheromones present; 4b had no effect of the positive pheromone ($\boldsymbol{\mu_{pos}}$=0); 4c had no effect of the negative pheromone ($\boldsymbol{\mu_{neg}}$=0). This allows an assessment of the roles of each pheromone in the ability of the simulated ants to find the food in its new location.

Modelling Experiments: Results

Normal foraging

The mean percentage of ants returning to the nest fed was 88%, sd=1.4%. The mean journey time was 30.1 sec, sd=0.11. Although this is statistically higher than the minimum possible journey time of 30 sec (t-test: t=4.26, *df*=19, p<0.001) due to the

mistakes in trail choice made by some simulated ants, this is still very close to the minimum. The mean number of visits to the end of the non-feeder branch is 0.10 per ant (sd=0.014). The branch leading to food was always positively attractive (fig. 3a). The non-feeder branch was almost always repellent; although it did occasionally become positively attractive, it never became as attractive as the feeder branch. The attractiveness of the non-feeder branch was significantly more variable than the attractiveness of the feeder branch: mean standard deviation of attractiveness of branch: feeder branch = 1.23, n=20, non-feeder branch = 8.01, n=20 paired t-test, t=13.04 df=19, $p<0.001$.

Pheromone strengths

In experiment 2h (fig. 4 a,b,c), in which there was no positive pheromone, significantly fewer of the ants returned to the nest fed than in experiment 1, the control with both pheromones (mean ±sd; no positive pheromone: 85.7% ±1.77; control: 88.3% ±1.38; χ^2=12.4, df=1, $p<0.001$). Journey time was also significantly longer without the positive pheromone (mean ±sd; no positive pheromone: 30.8sec ±0.1; control: 30.1sec ±0.1; t-test, t=15.2, df=18, $p<0.001$).

In experiment 2f, (fig. 4 d,e,f) in which there was no negative pheromone, again significantly fewer of the ants returned to the nest fed (81.3% ±23.0) than in the experiment 1 control. This very high variation in the proportion of ants fed, with a standard deviation of 23%, indicates great variability among trials. Examination of

individual trial data shows that in approximately 5% of trial, the non-feeder branch became more attractive than the feeder branch, and that the ants became locked into this incorrect choice (fig. 4f). Journey time was not significantly different without the negative pheromone (30.1sec ±0.1) compared to experiment 1 data with both pheromones (t-test, t=0.72, df=18, p=0.5).

In experiment 2g, where neither pheromone was used, the resulting proportion of ants fed (48.9% ±2.7) does not differ significantly from the 50:50 random expectation (χ^2=5.24, df=9, p=0.8).

Provided the effects of both pheromones are greater than zero, changes in relative concentration of the two pheromones has little effect on feeding success (fig. 5a,c) or journey time (fig 5b,d).

Traffic flow rate

There is a threshold traffic flow rate required for Pharaoh's ant colonies to form pheromone trails (Beekman et al., 2001). Varying flow rate in the simulations (see fig 6) shows that at flow rates of $^1/_4$ to 8 ants per time-step, over 80% of the ants return to the nest fed. Within this range there is no significant gradient t=2.35, *df*=5, p=NS). Below this range, a traffic flow rate of $^1/_8$ falls in the threshold region, with only 60% of ants returning fed. At even lower traffic flow rates below this, the proportions fed are not

significantly different from the 50:50 random expectation, which is what is seen when no pheromones are used ($^1/_{16}$ ants per time-step, χ^2=16.1, *df*=9, NS; $^1/_{32}$ ants per time-step, χ^2=4.9, *df*=9, NS).

Foraging in a dynamic environment

In experiment 4a, (fig. 7a) with both attractive and repellent pheromone present, there are no significant differences following the change in food location between these results and the results without a change in food location (experiment 1) either in the percentage successfully fed (χ^2=0.007, *df*=1, NS) or in journey time (t-test, t=1.18, *df*=18, NS). However in experiment 4b, (fig. 7c) without positive pheromone, foraging is significantly less successful. The mean percentage fed is 85.0% ±1.37 compared to 88.3% ±1.37 with both pheromones, (χ^2=19.9, df=1, p<0.001) and the journey time is 30.7sec ±0.16 compared to 30.1sec ±0.1, (t-test, t=11.54, df=18, p<0.001). An even more dramatic difference occurs when the negative pheromone is removed in experiment 4c (fig. 7e). Here the mean percentage fed is 48.5% ±1.2. Fig. 7f shows that without the negative pheromone the feeder branch remains attractive, despite the fact the food has been moved.

Discussion

Normal foraging

The simulations show that during normal foraging, that is with both attractive and repellent pheromones, the collective actions of the many individual workers maintain an attractive trail to the food, with the non-feeder branch being unattractive. This was to be expected. However, a novel result also emerged from these simulations of normal foraging. The attractiveness of the non-feeder branch is highly variable compared to the stable level of attractiveness of the branch leading to food. The non-feeder branch varies from highly repellent to slightly attractive. This instability is a result of the negative feedback which the repellent pheromone exerts on its own deposition. The non-feeder branch undergoes a drop in attractiveness when repellent pheromone is laid by an ant, and this then repels other ants from choosing that branch, preventing reinforcement. In the simulation it is usually only after the repellent pheromone has decayed to a low level that another ant takes the path and lays more pheromone. This leads to periodic sharp drops in attractiveness (when more repellent pheromone is laid) followed by a gradual rise in attractiveness (as the repellent pheromone decays). Our model therefore predicts that foraging Pharaoh's ant colonies should experience similar fluctuations in the proportion of foragers choosing a non-feeder branch. The attractive pheromone exerts positive feedback on its own deposition, so remains at a much more stable level.

Pheromone strengths

Experiment 2h demonstrated that as would be expected, the use of attractive pheromone increases foraging success and reduces journey time, as is evident when it is omitted from the model. The effect on journey time may seem slight (a mean increase of 0.7 sec), but this is equivalent to 2.3% of a foraging trip from the nest to the food and back. Our investigation of the relatives strengths of the attractive and repellent pheromones showed the same overall patterns over a range of relative strength.

Within our model the use of repellent pheromone also affects foraging success and journey time as shown by comparisons with simulations in which it is absent. Its absence has the strongest affect in those cases when a random switch in branch attractiveness occurs (fig. 4f), an effect which emerged from the model. These switches occur as a side-effect of the regulation of the attractive pheromone by positive feedback. In the simulation, as in reality, returning fed ants lay attractive pheromone on the way back to the nest. Occasionally, returning ants will take a wrong turn and go up the no-feeder branch. As a result this branch receives attractive pheromone even though there is no food. When the repellent pheromone is in use, this will cancel out the effect of any attractive pheromone which is laid on the wrong branch, preventing this branch from becoming attractive. In contrast, in the absence of the repellent pheromone (Experiment 2f) this incorrectly laid attractive pheromone may be reinforced by outbound trail-laying ants, via positive feedback. Through random fluctuations, this may lead to the maladaptive situation of the non-feeder branch becoming more attractive than the feeder branch. Without the repellent pheromone, it is difficult for the simulated ants to break out of this situation. {more here?}

Traffic flow rate

The investigation of ant traffic flow shows a threshold below which the colony cannot establish a trail to the food. Such a trail is necessary for the colony to favour the feeder branch over the non-feeder branch. At low traffic flow, pheromone decay overwhelms pheromone deposition, so that later foragers do not benefit from pheromones laid by earlier foragers. Foraging success is as low as in the experiment where pheromones were not used (2g). This agrees with previous results, which have shown both experimentally and analytically that small colonies of Pharaoh's ants cannot establish organised foraging trails (Beekman et al., 2001). Our model also predicts that above a certain threshold, increasing the ant flow will not increase foraging success. This is because some errors will always be made at bifurcations, just as some ants will always leave trails (Pasteels et al., 1986).

Traffic flow can have other effects which are not modelled here, for example crowding on the trails could cause more ants to make mistakes and choose the other, non-rewarding, branch (Dussutour et al., 2004) which would then make those ants more likely to find any alternative sources of food. Crowding at the source of food could also exert regulatory feedback on the laying of pheromones, as in some species of ant workers which cannot feed due to congestion at the food source cease to recruit

nestmates (Taylor, 1978; Wilson, 1962). Such effects could place an upper limit on the trail densities likely in nature.

Foraging in a dynamic environment

Most experiments and models investigating ant foraging use a static source of food (Beckers et al., 1992b; Lamb and Ollason, 1993; Nicolis and Deneubourg, 1999; Stickland et al., 1992; Taylor, 1977). Pharaoh's ants thrive in unpredictable environments, exploiting ephemeral food sources. We investigated this by changing the location of the food source during the simulation. Within our model both pheromones have a role in helping the ants make a switch from a formerly productive branch to a newly productive one. With only repellent pheromone and no attractive pheromone (experiment 4b), this switch occurs more slowly than with the attractive pheromone (experiment 4a), because ants which find the new food source cannot attract others to it without an attractive pheromone. The switch in foraging focus does occur however, because the repellent pheromone, closes off the formerly productive branch, so more ants take the other option and find the food, as predicted (Robinson et al., 2005). In contrast without the repellent pheromone, the switch to the newly productive branch never happens. The ants are locked in to the positive feedback loop attracting them to the previously attractive branch, and only a few ants which make mistakes find the food. This suggests that in real Pharaoh's ant systems, the repellent pheromone may have an important role in helping the ants adapt more quickly to changes in the food environment.

There may be other mechanisms which help ant colonies prevent these positive feedback lock-ins, including a minority of well informed trail-laying ants which make frequent U-turns (Hart and Jackson, 2006) and the polarity of the trail bifurcations (Jackson et al., 2004) which could help ants returning from a formerly productive branch to take the other outward-bound branch rather than the more attractive homeward bound one. Foragers modulating their pheromone deposition according to food quality can help ant colonies avoid being trapped at a less rewarding site when a more rewarding one is available (de Biseau et al., 1991; Nicolis and Deneubourg, 1999; Sumpter and Beekman, 2003). Despite this, in mass recruiting species such as *Lasius niger*, colonies may be unable to switch to a more rewarding site which is found later (Beckers et al., 1990). Other species use more individual recruitment mechanisms that promote switching to late-discovered better food sources or nest sites, e.g. group recruiting in *Tetramorium caespitum* (Beckers et al., 1990) and tandem-running in *Temnothorax albipennis* (Franks et al., 2008).

Conclusion

These simulations suggest some important roles for the repellent pheromone in the organisation of Pharaoh's ant foraging. The positive feedback mechanism (attractive pheromone) by which the Pharaoh's ant mediates its rapid responses to new sources of food has potential disadvantages when used alone. In particular, random errors can cause

the simulated colony to select an unproductive route or to be unable to switch their foraging effort to a new place when the location of food changes. Trail decay, which is usually proposed as the only negative control mechanism in pheromone foraging systems, can be insufficient to allow the colony to break out of a suboptimal foraging pattern. The repellent pheromone allows the colony to escape from ongoing suboptimal states caused by positive feedback loops, providing the system with added robustness to random fluctuations or changes in conditions, as well as aiding trail choice.

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Figure legends

Figure 1. Schematic of model. The three general behavioural states are indicated in the boxes. Each state has an action associated with it (---►) and the states are connected by transition actions (—►). When *nest ants* leave the nest they become *unfed foraging ants*. These agents search for food until they either find it, whereupon they become *fed foraging ants*, or find the nest instead, whereupon they become *nest ants* again. *Fed foraging ants* search for the nest until they too find it and become *nest ants*.

Figure 2. The four-cell environment in which simulated foraging takes place. In the simulations, θ_B =60°; θ_S =150°. Outward bound agents therefore deviate from their path by 30° when they enter a branch; agents returning along a branch deviate by 30° if they take the stem, or 150° if they take the other branch.

Figure 3. Relative attractiveness of the two branches over the course of a simulation experiment. 3a shows the means of 20 trials, ± standard deviation; b shows a data set from a typical trial.

Figure 4. Relative attractiveness of the two branches in the absence of one of the two pheromones. 4a. Experiment 2h, (no positive pheromone present) mean ±sd, over 10 trials; b&c show example data sets. 4b. Experiment 2f (no negative pheromone mean ±sd, over 10 trials; e&f show example data sets, including a switch in branch attractiveness (4e).

Figure 5. Effect of relative pheromone strengths on foraging success and journey time. Percentage returning to the nest fed (a&c) and journey time (b&d), mean ± sd, over 10 trials, comparing a range of strengths of positive pheromone (with negative constant at 26) (a&c) or negative pheromone (with positive constant at 2) (c&d).

Figure 6. Effect of traffic flow on foraging success. Percentage of ants returning fed, mean ± sd, over10 trials. On the x-axis is the logarithm (base 2) of ant flow, i.e. ranging from 1/32 to 8 ants per time-step. The dashed line indicates the random expectation.

Figure 7. Results of experiment 4: foraging in a dynamic environment. At 600 seconds, the position of the food has been changed from the 'feeder branch' to the 'non-feeder branch'. 7a: experiment 4a, (both pheromones present) mean values over 10 trials ± standard deviation (given for every other point, for clarity); b is an example data set. 7c: experiment 4b, (without positive pheromone) mean ± sd; d is an example data set. 7e: experiment 4c, (without negative pheromone) mean ±sd; f is an example data set.

Symbol	Summary	Value	Source
θ_B	Angle between branches (see fig 2)	60˚	The angle between outward branches in Pharaoh's ant trail bifurcations ranges from 50˚ to 60˚ (Jackson et al., 2004).
θ_S	Angle to stem (see fig 2)	150˚	(360˚- θ_B)/2
τ	Time-step duration	6 sec	The mean speed at which foraging Pharaoh's ants travel is 15.1mms^{-1}, s.d.=5.2mms^{-1}(Robinson, unpubl. data). The branches and stem on the experimental apparatus used were 90mm long. τ = 90mm/15mms^{-1}
φ	Traffic flow rate	1 ant per 3 sec (2 ants per τ)	Empirically measured (see Suppl. Info) **Explored in Simulation experiment 3**
ε_θ	Error rate at angle of deviation (the proportion of ants which choose a branch at random at a bifurcation)	1% when θ=120˚ 5% when θ=30˚ (see fig 2)	Empirically measured (see Suppl. Info) **Explored in Simulation experiment 4**
μ_{pos}	Effect of positive pheromone	2 arbitrary units	**Explored in Simulation experiment 2**
μ_{neg}	Effect of negative pheromone	-26 arbitrary units	Estimated relative to effect of positive (see Suppl. Info) **Explored in Simulation experiment 2**
μ_{detect}	Threshold of detection	1 arbitrary unit	Estimated relative to effect of positive (Jackson, 2005)
λ	Pheromone decay constant	0.4075	Estimated from (Robinson et al., in press) (see Suppl. Info)

Table 1. The values and derivations of the constants and parameters used in the simulation experiments.

Experiment	Positive pheromone μ_{pos}	Negative pheromone μ_{neg}
1	2	26
2a	2	20
2b	2	14
2c	2	8
2d	2	2
2e	2	1
2f	2	0
2g	0	0
2h	0	26
2i	1	26
2j	2	26
2k	8	26
2l	14	26
2m	20	26
2n	26	26

Table 2. The strengths of the positive and negative pheromones used in experiments

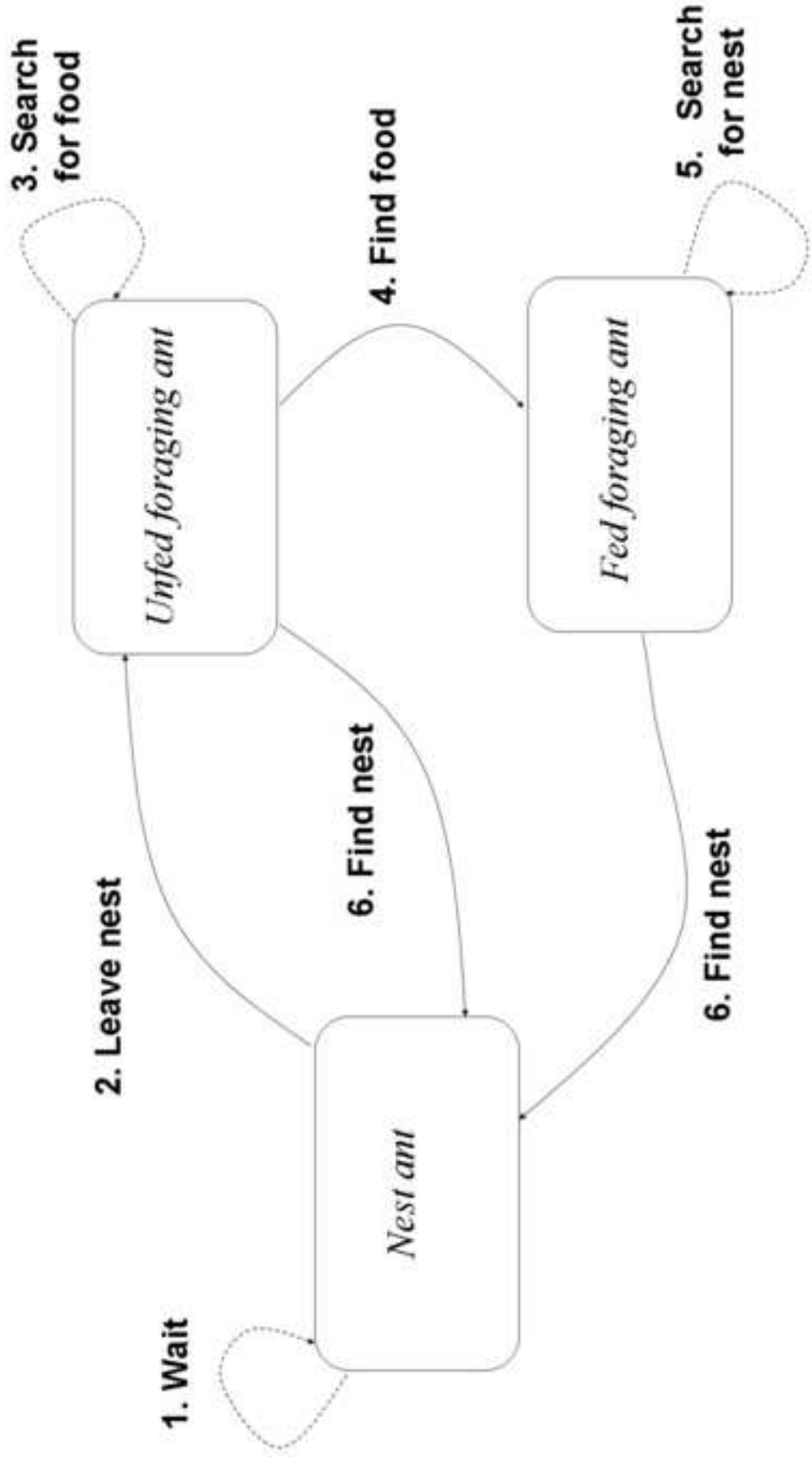
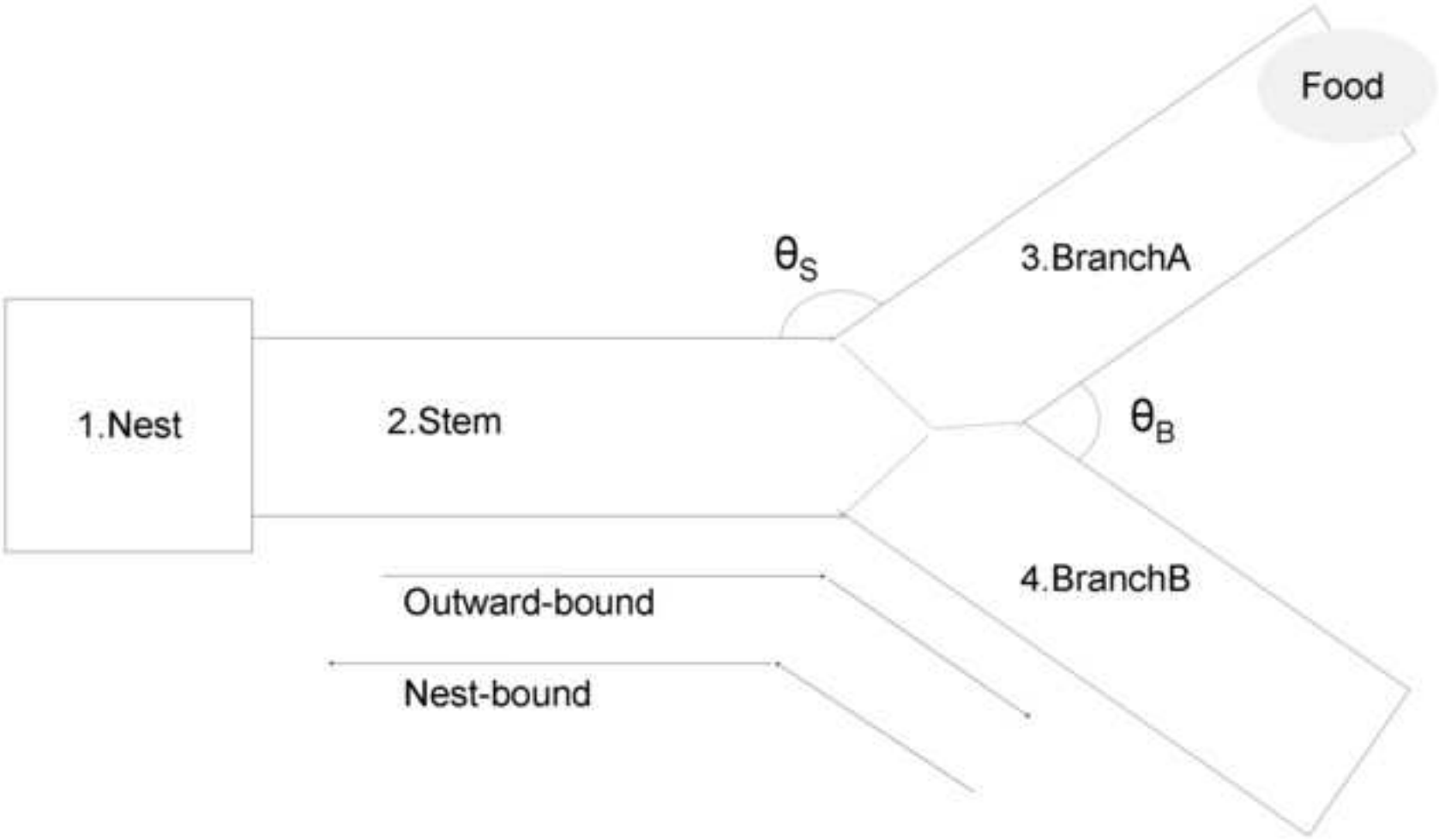


Figure 1: Model scheme

Figure 2: Modelled Environment



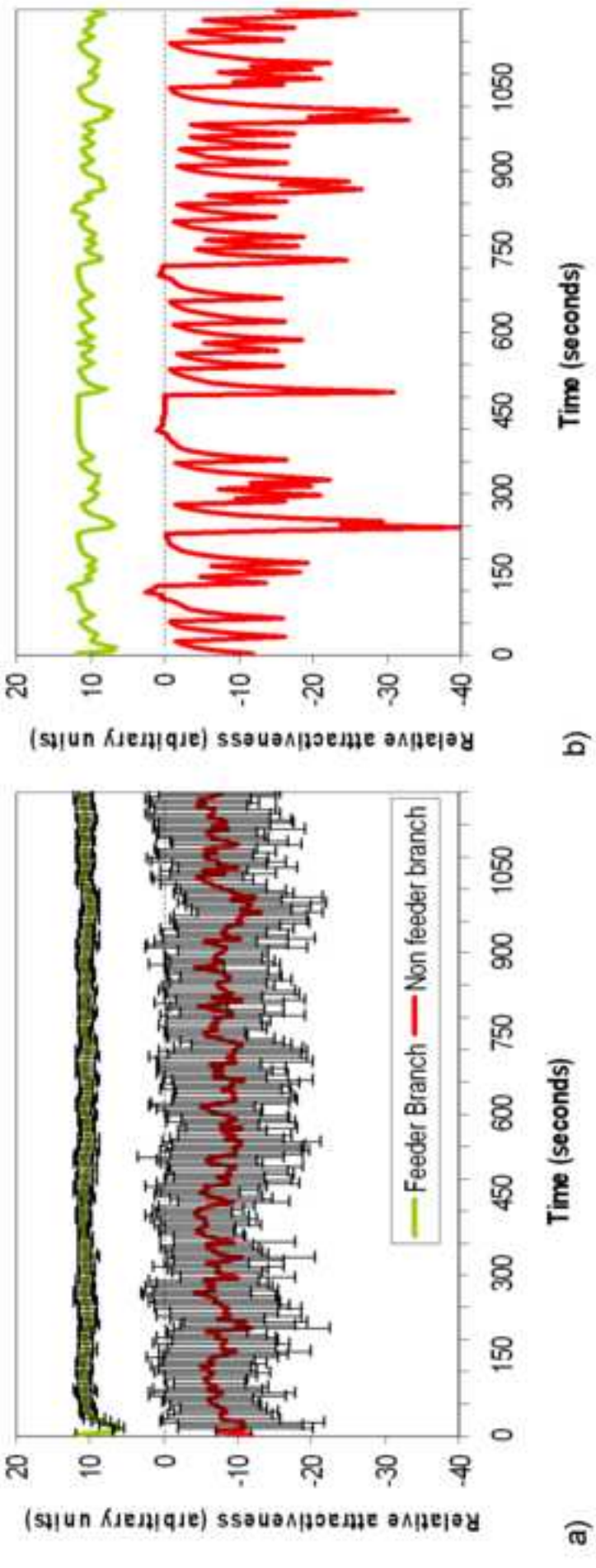
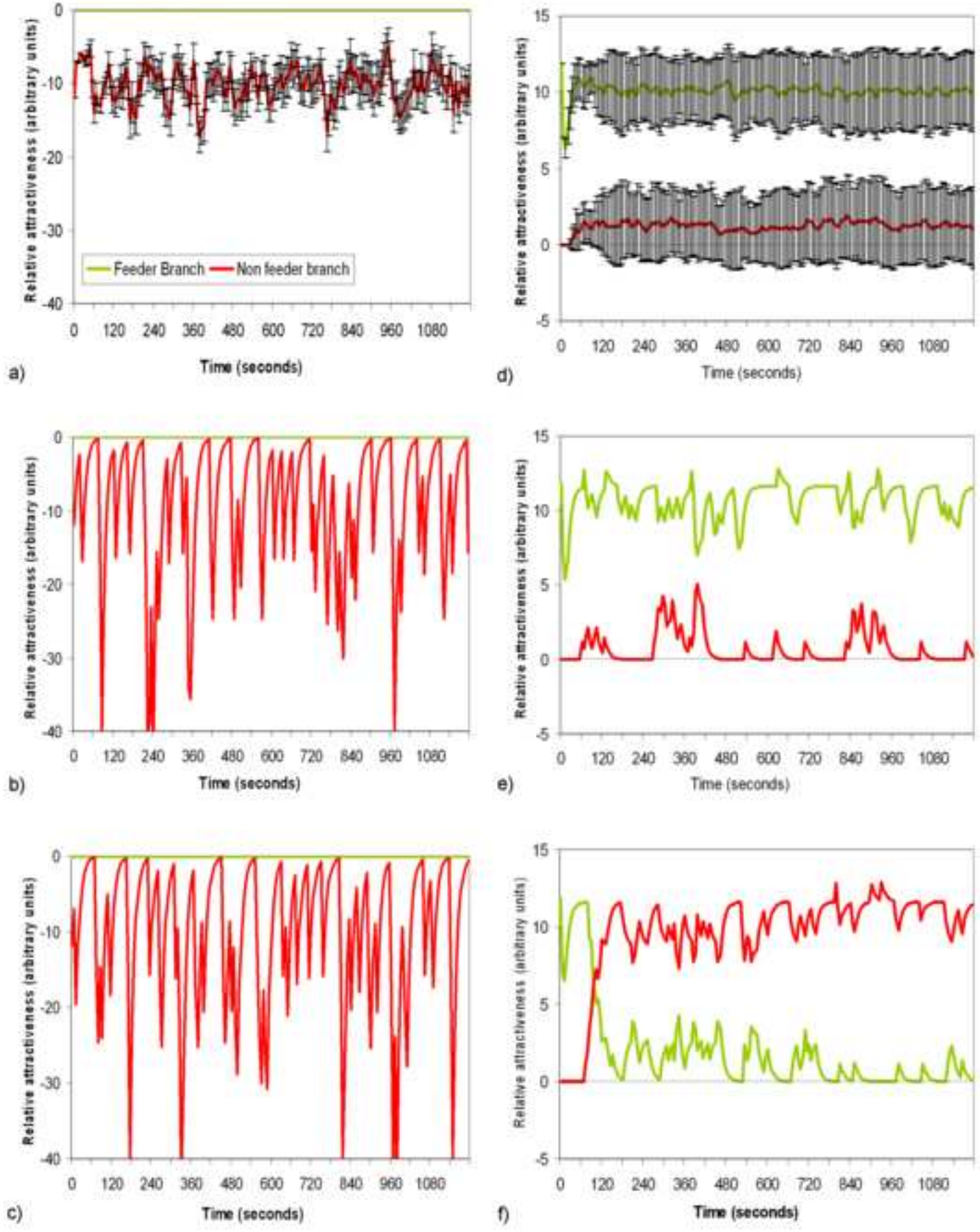


Figure 3: Experiment 1

Figure 4: Experiment 2



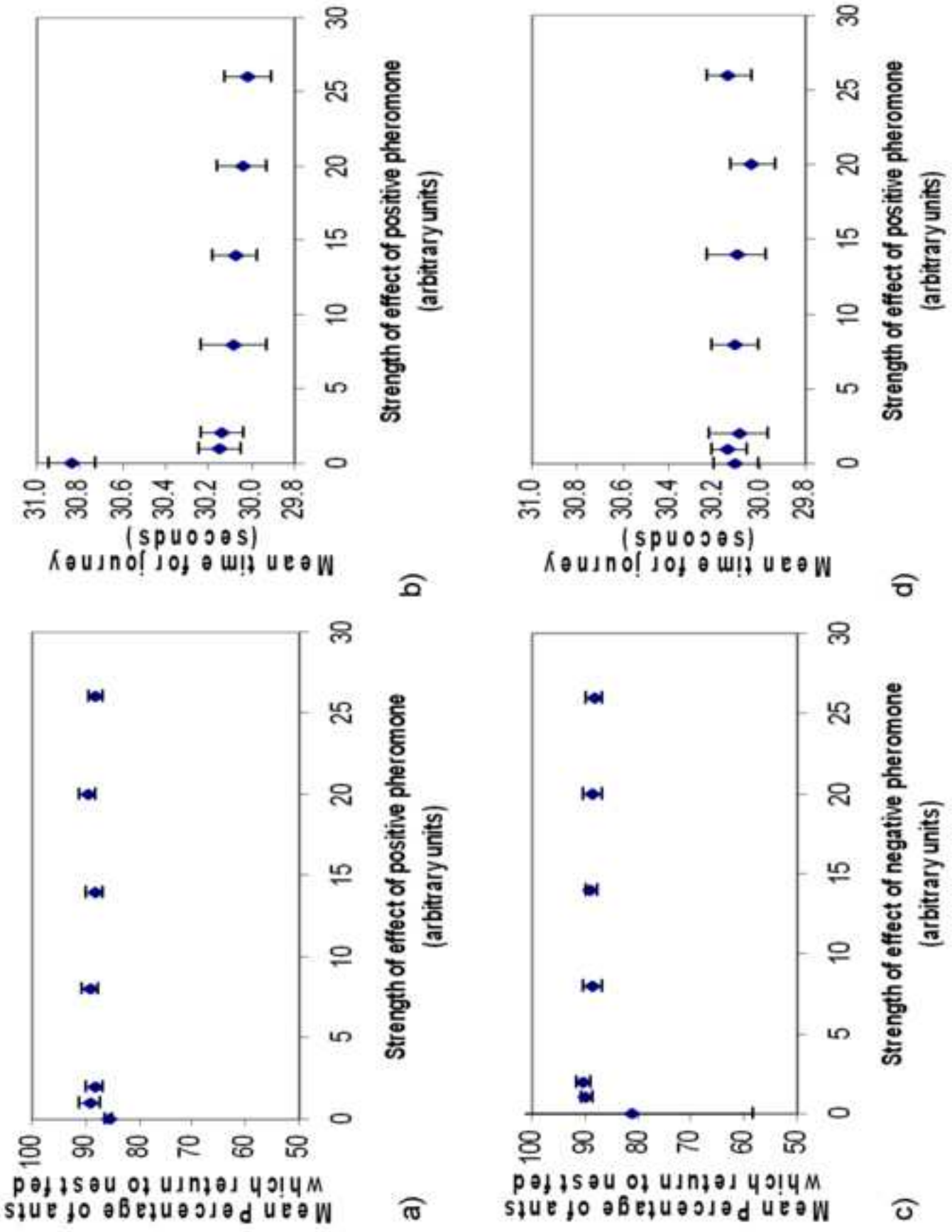


Figure 5: Experiment 2b

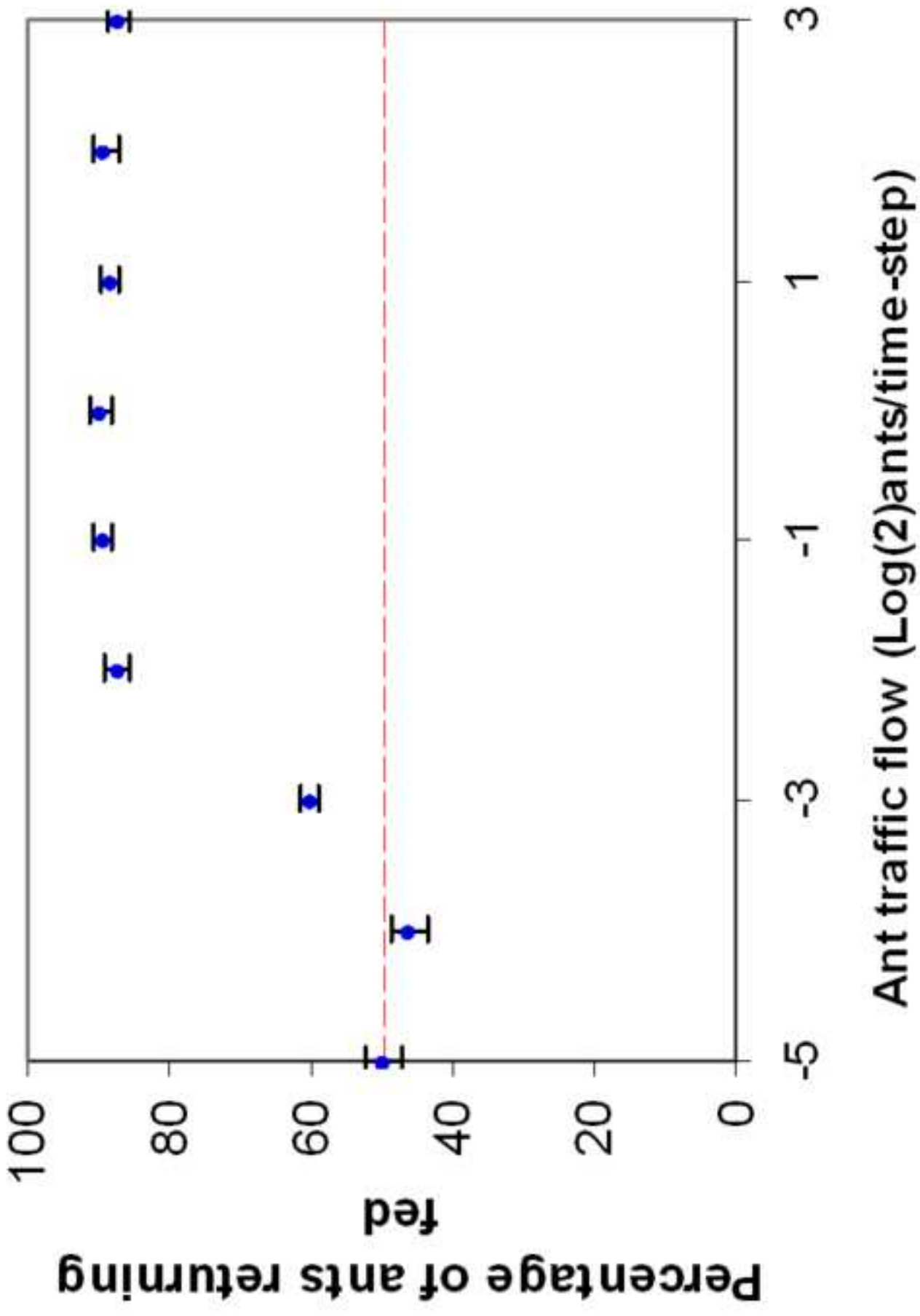


Figure 6: Experiment 3

Figure 7: Experiment 4